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Predicting the Growth Potential of a Shallow, Warm-Water Sport Fishery: A Spatially Explicit Bioenergetics Approach

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PREDICTING THE GROWTH POTENTIAL OF A SHALLOW, WARM-WATER SPORT FISHERY: A SPATIALLY EXPLICIT BIOENERGETICS APPROACH

by

Samuel K. Dahle

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ABSTRACT

Predicting the Growth Potential of a Shallow, Warm-Water Sport Fishery:

A Spatially Explicit Bioenergetics Approach

by

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Capturing the range of fish consumption and growth potential of large, heterogeneous lentic systems can be challenging due to strong gradients in productivity, the diversity of habits types present, and in some cases, site-specific water quality issues. Cutler Reservoir (Utah, USA) displays a high degree of spatial and temporal variation in physical conditions and potential water quality limitations for fish, including high summertime water temperature and large, diel fluctuations in dissolved oxygen concentrations. The combination of bioenergetics modeling and GIS spatial analysis offers a promising interface for quantifying the fish consumptive and growth potential across a spatially and temporally heterogeneous system like Cutler Reservoir, as well as identifying the role of potential water quality impairment on fish population abundance and condition. Within a bioenergetics framework, we combined empirical field estimates of fish growth and diet composition with a novel use of Thermal Remote Imaging (TIR)

as a measure of spatially explicit thermal regime across a very large spatial scale (9,601,200 m^2). We used these data inputs and a Geographic Information System (GIS) to generate spatially explicit, high-resolution maps of the growth potential of the primary sport fishes of Cutler Reservoir across spring, summer, and autumn seasons. The predicted growth potential of these fishes varied widely according to spatial and temporal differences in temperature and food availability, acting in concert with species-specific physiological tolerances and habitat preferences. Walleye (*Sander vitreus*) and black crappie (*Pomoxis nigromaculatus*) experience high growth potential throughout much of the reservoir during spring and fall, but are constrained to small thermal refugia during the heat of the summer. In contrast, channel catfish (*Ictalurus punctatus*) growth potential is low during spring and fall, but peaks strongly during the warm summer period. The proportion of habitat suitable for each primary sport fish ranged from highs of > 90% for channel catfish for most of the summer season to lows < 5% for crappie in July. Our approach provides a useful tool for analyzing factors that control fish growth in complex water bodies such as Cutler Reservoir as well as identifying the role of water quality in structuring fish community composition.

(48 pages)

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Kirk Dahle

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INTRODUCTION

The development of quantitative methods for measuring habitat suitability is a central, but challenging task for aquatic biologists (Downing et al. 1990; Boisclair 2001; Rosenfeld 2003). The difficulty of measuring habitat suitability is made harder by the heterogeneity often present in large lentic systems. Ultimately, a measure of habitat quality is necessary to accurately predict predator-prey relationships, fish production, and sustainable stocking or harvest quotas (Baldwin et al. 2000; Mazur et al. 2007). Fish growth potential, which is generally defined as the expected growth rate of a fish in a specified volume of water with known biological and physical characteristics, has provided one such metric of habitat suitability (Brandt et al. 1992; Mason et al. 1995; Luecke et al. 1999). Temperature, a key abiotic variable, and food availability, a key biotic variable, act in concert with species specific physiological processes to directly influence the individual growth rate of a fish (Kitchell 1977; Stewart and Ibarra 1991; Hanson et al. 1997). Slight temperature deviations above or below the physiological thermal optima of a species can result in increased metabolic demands and physiological stress, subsequently resulting in a reduction of individual growth rates (Jackson et al. 2001). In addition, optimal thermal conditions must be coupled with sufficient food resources to achieve maximum growth rates and meet the consumption demands of the fish (Hansen et al. 1993; Hayes et al. 2000). As a result, the quantification of fish growth potential demonstrates a fish's response to environmental conditions, activity level, and metabolic requirements, and thus serves as an index of habitat quality.

Fish bioenergetics provides a reliable tool for measuring the physiological response of a fish to its environment, and thus allows the quantification of growth

potential (Hewett and Johnson 1992). Bioenergetic modeling relies on concrete thermodynamic principles and is based on the mass balance equation: *Growth* = (*Consumption – Respiration – Specific Dynamic Action – Excretion – Egestion*) (Kitchell 1977). Consequently, bioenergetic model outputs are relatively robust (Figure 1; Hansen et al. 1997), and deviations between predicted growth potential and observed growth rates can be used to refine the accuracy of model inputs such as diet and thermal history, or our quantification of physiological processes (e.g., allometric scaling; Boisclair and Sirois 1993; Ney 1993; Slaughter et al. 2004). Further, a bioenergetics approach can aid in refining our understanding of the relative importance of habitat variables and biological function (Boisclair 2001). These model predictions of fish growth or consumption can then be made more accurate through finer scale measurements of key model inputs (thermal history, diet), as well as more precise estimation of species specific physiological parameters (Lasker 1978; Ney 1990; Slaughter et al. 2004; Trudel and Welch 2005).

Coarse spatial and/or temporal resolution of temperature and food availability estimates represent some of the greatest sources of uncertainty for predicting fish growth potential, especially in large, heterogeneous water bodies (Brandt et al. 1992; Brandt and Kirsch 1993). In order to address this challenge, fisheries scientists have increasingly moved from the simple, deterministic approach of Winberg's (1956) original bioenergetics equation to models that attempt to more explicitly account for the heterogeneity of aquatic habitats. Incorporation of spatially defined higher resolution thermal and consumption data into models predicting fish growth rate, fish production,

predator-prey interactions, and habitat quality have substantially increased the relevance of bioenergetics predictions (Goyke and Brandt 1993; Mason and Brandt 1996; Niklitscheck and Secor 2005). Although spatially-explicit bioenergetics models have been criticized for their complexity and potential for error propagation (Ney 1990; 1993), they have been effective in illuminating the complex interaction between biotic and abiotic habitat variables that dictate the ability of aquatic environs to support fish growth (Brandt and Kirsch 1993).

In shallow aquatic environments such as streams or estuaries, Boisclair (2001) describes a bioenergetics approach using a two dimensional tile arrangement that is suitable for addressing the complex spatial nature of these aquatic landscapes. Each tile represents a homogenous unit of habitat, and the sum of habitat units constitutes a habitat mosaic. Collecting the spatially defined bioenergetic model input data needed to characterize this habitat mosaic requires a multidisciplinary approach. Large pelagic environments present the opportunity to employ a combination of hydro-acoustic data collection and traditional limnological sampling techniques. With the aid of geographic information systems, these data have been used to create detailed maps of spatially defined growth potential (Brandt et al. 1992; Goyke and Brandt 1993). Unfortunately, however, the physical complexities of spatial data collection in streams and large littoral habitats (e.g. complex riverine topography, macrophyte crowded shallows) have largely prevented their analog in this respect.

Thermal Infrared (TIR) Imaging presents a more spatially defined approach to describing the temperature available to a fish in a given environment. Thermal Infrared

Imaging facilitates the collection of high resolution, spatially-continuous thermal data (Torgerson et al. 2001). Although the application of TIR imaging to stratified three-dimensional aquatic systems presents challenges (Hook et al. 2004), shallow, lentic systems that mix continuously are ideal candidates for the use of thermal remote sensing techniques. These shallow, mixed lentic systems display two-dimensional thermal heterogeneity similar to that found in stream systems and can be mapped with TIR to a relatively high degree of accuracy and over a very large scale (Torgerson et al. 1999, 2001; Faux et al. 2001). As such, TIR imaging provides a tool capable of generating continuous thermal data sets that capture fine scale spatial temperature fluctuations for incorporation into bioenergetics modeling.

We developed a two-dimensional, spatially defined bioenergetics approach to estimate the growth potential of a shallow, warm-water reservoir using traditional fish and limnological sampling techniques, in combination with continuous, remotely-sensed thermal data. We spatially defined our bioenergetic model inputs and results using a GIS framework, and then produced a synoptic view of spatially defined growth potential for the system. The primary objective was to generate a spatially defined map of the growth potential of the predominant game fishes of a shallow, mixed reservoir, Cutler Reservoir, Utah, (channel catfish, crappie, and walleye). We focused on temperature, as this variable can be quantified with a high degree of spatial resolution using remotely-sensed data, preliminary investigation indicates that temperature is the limiting factor for these species in Cutler Reservoir, and temperature is one of the primary drivers of habitat suitability for fishes in general (Crowder and Magnuson 1983; Stewart and Ibarra 1991).

METHODS

Study Site

Cutler Dam, located in northern Utah, impounds the waters of the Bear, Logan, and Little Bear Rivers, as well as several other small tributaries creating Cutler Reservoir (Figure 1), with a capacity of 23,802 acre feet and a surface area of 9,601,200 m2. Cutler Reservoir reached its current full pool in 1927. Since that time, sedimentation has homogenized the bathometry of the water body resulting in average depths of less than one meter in the southern half of the reservoir and 1.5 - 2.5 m in its northern reaches. Under current operation the reservoir fluctuates less than 0.5 meters annually with a mean surface elevation of 1343.6 m. Cutler Reservoir is a cool, polymictic system that mixes frequently during mild to moderate wind events. Stratification, if present at all, generally persists less than 3 days and occurs only in the upper 0.5 m. Winter-time lows of 0-1^{o}C and ice cover are common, while mid-summer surface temperatures reach 20-30^{o}C depending upon location. Shoreline habitat is predominated by inundated macrophytes, specifically cattails (*Typha latifolia)* and hard stem bulrush (*Schoenoplectus acuts*).

Cutler Reservoir is a eutrophic water body (summer-time total Kjeldahl nitrogen concentrations generally < 1 µg/L, total phosphorus < 0.2 µg/L) with summertime chlorophyll *a* concentrations above 50 µg/L. Over the duration of this study dissolved oxygen conditions did not appear to be limiting fish (dissolved oxygen > 4 µg/L). However, reports of summertime fish kills (Utah Division of Wildlife Resourses, UDWR, personal communication) during low runoff years suggest that dissolved oxygen depletion may occur periodically. The zooplankton biomass of Cutler Reservoir is

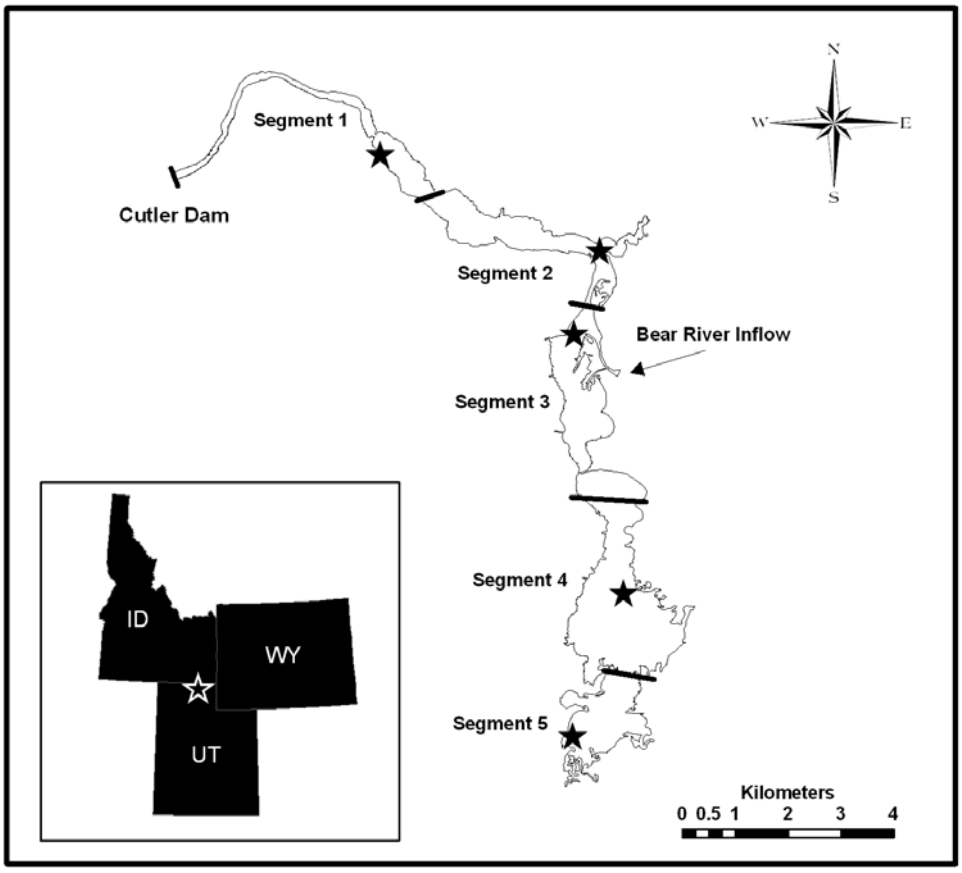

Figure 1. Map of the study area. Segments 1-5 were sampled intensively during spring, summer, and autumn of 2006; Reservoir segment boundaries are defined by black bars. Black stars indicate temperature logger locations.

diverse and is dominated by Moinids during all seasons followed by Daphnia spp., and copepods, respectively.

Cutler Reservoir contains multiple game fish species, including black bullhead (*Ameiurus melas*), black crappie (*Pomoxis nigromaculatus*), channel catfish (*Ictalurus punctatus*), and walleye (*Sander vitreus*). Potential forage species include bluegill (*Lepomis macrochirus*), carp (*Cyprinus carpio*), fathead minnow (*Pimephales promelas*) and green sunfish (*Lepomis cyanellus*).

Study Design

In order to capture the range of abiotic and biotic conditions, as well as the distribution of fish within Cutler Reservoir, we sampled five index segments (1-5) during 2005 and 2006 (Figure 1). Where possible, sample locations were chosen near historical Utah Division of Water Quality (UDWQ) sampling stations in order to increase the available data set. We conducted pilot sampling during June and August of 2005 to determine an optimal sampling strategy. We then implemented a standardized sampling protocol during spring (May), summer (July), and autumn (October) of 2006.

Fish Sampling

Our standardized sampling protocol consisted of a combination of three experimental gill nets (1.8m x 40m; 8 panels containing 19-64mm bar mesh in 6mm intervals), three trap nets (1.8m x .8m rectangular mouth, multiple baffle, with 30m leads attached), boat electro-fishing (Coffelt WP 15 boat electro-fisher), and beach seining (1.2m x 10m, 4mm mesh). We sampled each reservoir segment using randomly distributed gear for one night during each sample period. We placed all passive sampling gear before sunset, recorded its location using a handheld GPS unit, and retrieved nets the following morning, thereby encompassing two crepuscular periods. In addition, we conducted beach seining during both morning and evening time periods, typically conducting 4-8 seine hauls in each segment during each sample period. Lastly, we conducted all electro-fishing at night by shocking 3-6, 100 meter transects in each reservoir segment during each sample period. Captured fish were identified to species,

weighed, measured (nearest mm total length), and released. We retained a sub sample of captured fish for laboratory age and diet analysis.

Thermal Data Collection

We used three forms of sampling to describe the thermal characteristics of Cutler Reservoir during 2006. First, we placed one digital temperature logger (Hobo Pendant temp 64k) 0.5 m below the surface in a representative location of each sample segment (*n = 5*) and set temperature loggers to record temperature every 0.5 hours. To ensure that selected logger locations were representative of each reservoir segment we sporadically placed temperature loggers throughout the reservoir for use in other studies and then compared the data from these temporary positions with our fixed sample site. Second, in order to capture the spatial heterogeneity of the thermal environment, we used two forms of remote sensing, which allowed us to expand our thermal data into a continuous, spatially explicit data set. During summer sampling we used helicopter-mounted Thermal Infrared Imagery (TIR) to capture a synoptic, one time view of the thermal habitat of the reservoir with extremely high resolution (pixel size = 3m) . We ground truthed aerial TIR data using in-situ temperature loggers (n = 12) (Torgerson et al. 1999; 2001; Faux et al. 2001). Lastly, we obtained Landsat 5 National Landsat Archive Processing System (NLAPS) band six (thermal band) data that corresponded with our spring and autumn sampling dates (pixel size 30m). We converted Landsat thermal band data to degrees Celsius using the algorithm developed by Barsi et al. (2003) and cross validated this data with in-situ temperature loggers to test and correct for systematic bias.

Fish Growth

We generated length frequency histograms in order to determine annual growth rates for walleye, black crappie, and channel catfish for each reservoir segment. Size-at-age data was then validated for black crappie and walleye using scale and otolith aging, respectively. Catfish sample sizes were sufficiently large, and cohorts were well defined using length frequency data requiring no additional age validation.

Diet Analysis

We analyzed stomach contents for prey abundance and composition. We enumerated fish and zooplankton remains on a sub-sample of target fish collected in each segment, and identified prey items to species when possible. We enumerated terrestrial and aquatic invertebrates and identified individual specimens to order. After identification and enumeration, we measured and weighed all stomach contents (blot-dry wet weights to nearest 0.001g) in order to quantify the size fraction of prey items selected by fish and to calculate diet proportion by wet weight.

Bioenergetic Modeling

We evaluated overall growth potential for Cutler Reservoir as well as relative differences in growth potential across segments given inherent differences in thermal history and diet proportions using the Wisconsin Bioenergetics model 3.0 (Hansen et al. 1997; Figure 2). We modeled walleye growth using physiological properties from Madon and Culver (1993), and we synthesized black crappie physiological properties, substituting adult bluegill parameters (Kitchell et al. 1974) with adjusted optimal and

thermal maximum respiration and consumption temperatures (Jobling 1981), following recommendations from Hansen et al. (1997). Channel catfish physiological properties were generated by substituting flathead catfish physical parameters (Roell and Orth 1993) with adjusted optimal and maximum temperatures, as described above.

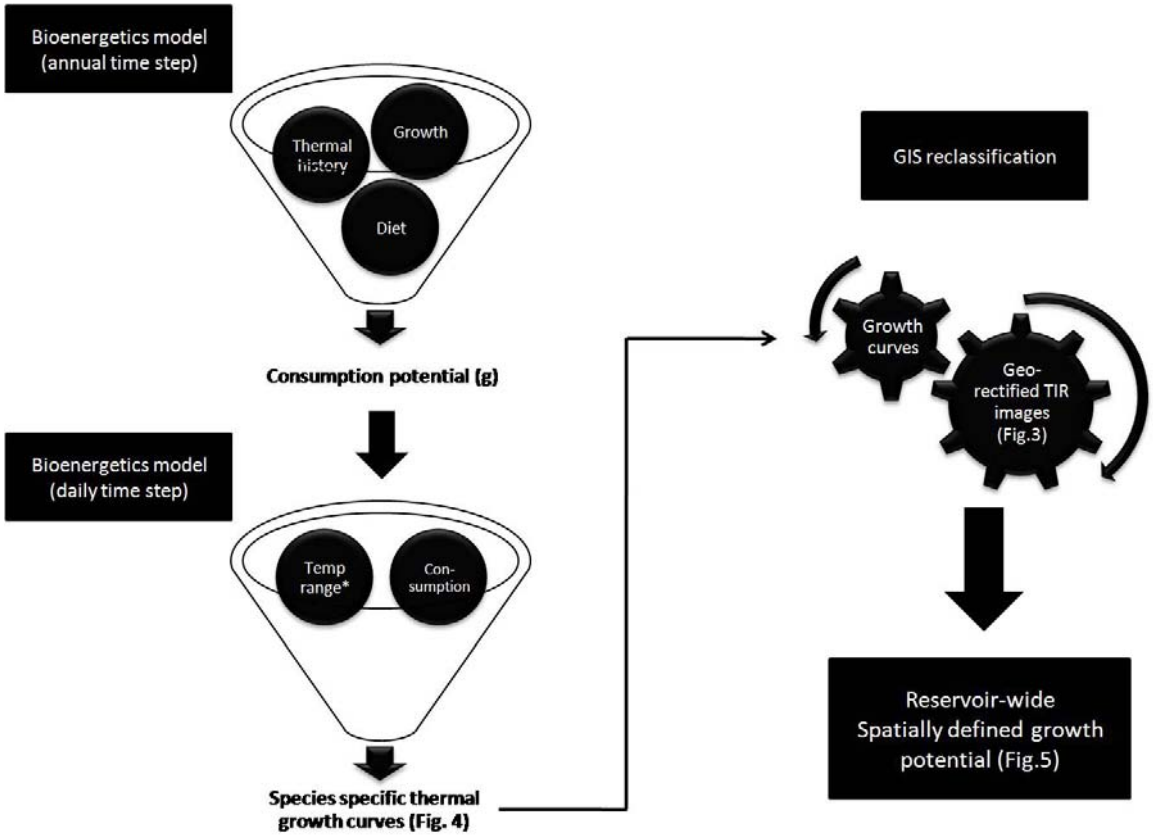

Figure 2. Schematic diagram of data processing steps used to generate spatially defined growth potential maps. Annual and daily bioenergetics models were based on the Wisconsin bioenergetics model (Fish Bioenergetics 3.0, Hansen et al. 1997). Inputs for our annual bioenergetics model represent site-specific data collected at sites 1-5 during 2006.

* Represents the temperature range experienced by our target species during the modeling period. Geo-rectification and reclassification were completed with ArcGIS 9.2.

We first ran model simulations for each individual reservoir segment incorporating site-specific growth, seasonal diet composition, and thermal history using temperature data collected with temperature loggers. These segment specific simulations encompassed the time period from April 1 to October 1, representing the summer growing season and the period of time when water temperatures exceed 10^{o}C. We assumed fish attained 80% of their annual growth during this period and used these estimates as our growth (g) input for bioenergetics modeling (Vatland et al., 2008). We used the output of estimated consumption (g/individual) from these segment specific model runs to parameterize consumption rates for the target species (hereon referred to as field estimated consumption). Second, we generated species-specific thermal growth curves by running bioenergetics simulations on a one day time step for the range of temperatures present in the TIR data. We modeled the average individual of each target species (channel catfish 400g, black crappie 100g, and walleye 1000g), to generate species-specific thermal growth curves. We held individual consumption potential as a fixed variable, as estimated from the segment-specific model runs described above, and allowed the bioenergetic model to scale consumption based on thermal conditions. In order to evaluate the sensitivity of the model to consumption rates, we bracketed the consumption estimate from the segment-specific simulations (field estimated consumption) by ± 20% and re-ran the simulations to generate upper and lower bookends for our thermal growth curve estimates.

We used these species-specific thermal growth curves to classify the growth potential of the TIR data for each of the three target species. Daily growth curves

provide an estimate of growth potential in g/individual/day based on temperature and field estimated consumption. Using ArcGIS 9.2, we reclassified the TIR images from oC to growth potential (g/individual/day) by reassigning each pixel in the image with the according growth potential estimate generated by the daily time step bioenergetics model (Figure 1). Using this approach we were able to generate synoptic maps of spatially defined (3-30m pixel size) growth potential estimates for the three target species. Additionally, we calculated the seasonal mean, and standard deviation, of predicted growth potential for each of the target species and generated a Cumulative Frequency Distribution (CFD) of available habitat vs. modeled growth potential for each target species and season. Lastly, we extracted seasonal, segment-specific, mean growth potential for each of the target species and used linear regression to regress this metric against the corresponding Catch Per Unit Effort (CPUE) estimates from field sampling.

RESULTS

Fish Sampling

We were able to reliably capture all three target species using a combination of active and passive fish sampling techniques. We conducted 680 hours of gill netting, 740 hours of trap netting, seined 800 m2, and electro fished over eight kilometers of Cutler Reservoir during the 2006 sampling effort. We feel our fish catch data is representative given that sampling was conducted during spring, summer, and autumn, and spanned all available habitat types. Further, fish proportional biomass (individual species catch / total catch) remained relatively stable across the three sample periods in 2006 (Figure A.1). In contrast, the total catch per unit effort varied considerably between sample dates with summer catch rates nearly double that of spring and autumn catch. Carp dominated the catch at all locations and during all sample periods, averaging 68% (1 SE = 1.32) of the total catch. Catfish biomass was also substantial, averaging 18.5% (1 SE = 0.57). Walleye biomass was much smaller averaging 6.4% (1 SE = 1.14). Black crappie constituted only 2.3% (1 SE = 0.67) of our total catch biomass during 2006.

Thermal Data

Cutler Reservoir demonstrates a dynamic and heterogeneous thermal environment. Daily average temperatures, as recorded at temperature loggers, ranged from 6.7^{o}C (segment 5, April 1) to 28.7^{o}C (segment 3, July 23). On July 30, 2006 temperatures ranged from 18^{o}C to 34^{o}C (Figure 3). Daily temperature fluctuation was considerable during the sampling period, with up to 5^{o}C diel variation. However, daily

average temperatures closely corresponded to TIR thermal data (average difference = -0.5^{o}C, 1 SE = 0.69^{o}C). Further, daily average temperatures from dispersed, temporary placed, temperature loggers closely matched the daily averages from our fixed logger stations in the corresponding reservoir segment supporting that these sites were representative of each segment. Based on the high level of agreement between the TIR thermal data and the temperature logger data, no adjustments were made to the TIR data sets prior to their use in bioenergetics modeling.

All TIR images display a general warming pattern in water temperature moving from south to north within the reservoir. Cool inflowing water from the Logan and Little Bear Rivers are clearly visible in the southern portions of the water body (Figure 3). These two streams enter the reservoir at 20-23^{o}C during summer and warm to 27-28^{o}C within 2km of their inflow point as they spread across the broad, shallow, southern portion of the water body (Segments 4 and 5). Additionally, although to a lesser extent, cool water inflows from the Bear River can be observed mixing with warm reservoir waters from the confluence of the Bear River at Segment 3, north of the upstream boundary of Segment 1. We observed a pattern of increasing water temperature with residence time in the reservoir in all TIR images.

Fish Growth

Fish growth rates were variable across both species and sites within Cutler Reservoir (Table 1). However, in this system, game fish grow at or above average rates for similar water bodies (Carlander 1969; Galinat and Willis 2002; Murphy et al. 1991). Walleye demonstrated particularly fast growth rates, with some individuals reaching 1 kg

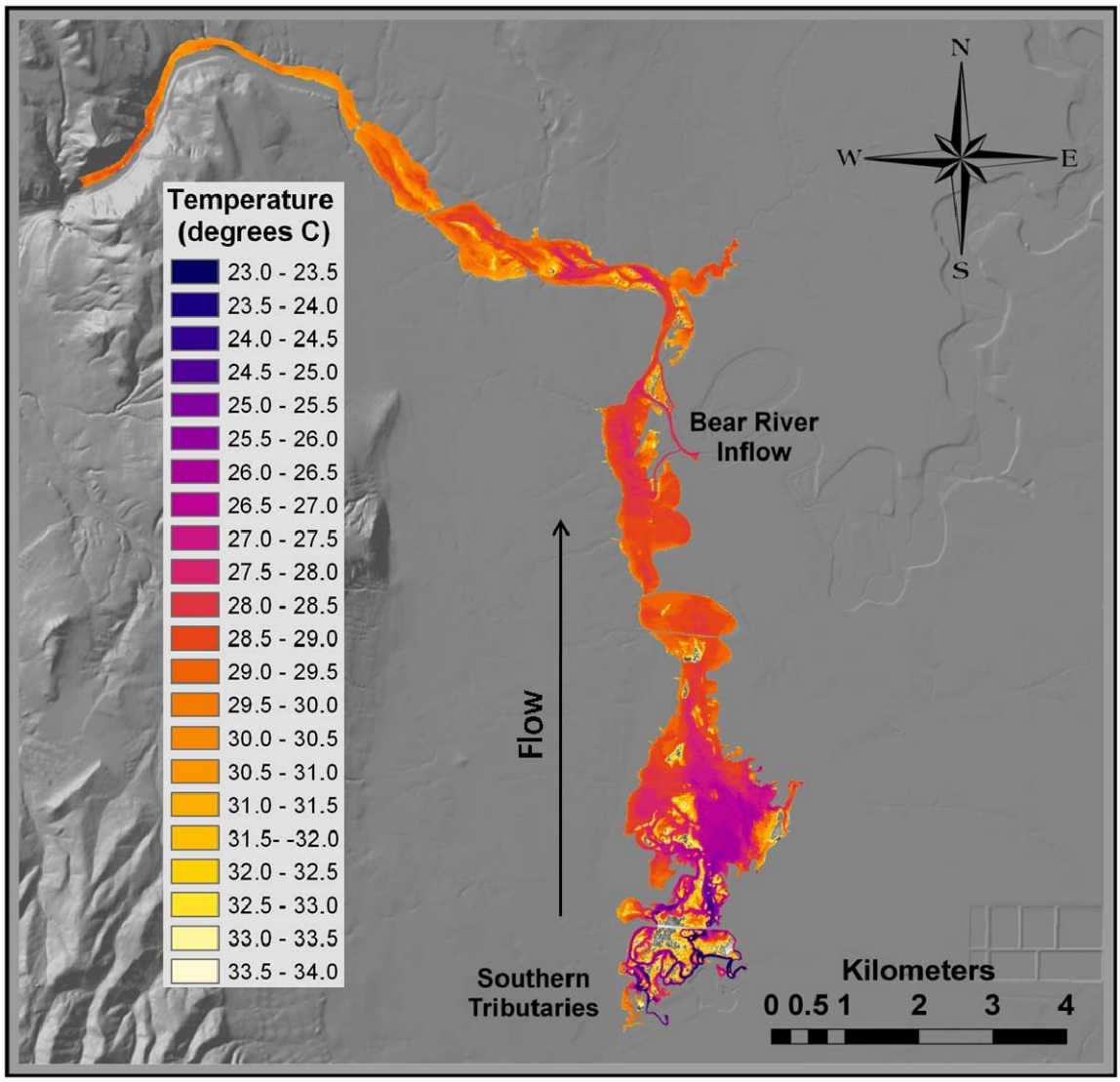

Figure 3. Thermal Infra Red (TIR) image of study site. Synoptic, three meter resolution, thermal image of Cutler Reservoir taken July 30, 2006 showing temperature variation within the study area.

Table 1. Segment and age-specific, seasonal (April 1–October 1) growth estimates (in grams) used for bioenergetic modeling. Estimates are based on length-frequency histograms and fish ageing data.

Walleye			
Age 1-2	Segment	Start Weight	80% end weight
	1	546	814
	2	583	854
	3	470	682
	4	628	868
	5	688	928
Age 2-3	Segment	Start Weight	80% end weight
	1	950	1150
	2	1000	1220
	3	800	1000
	4	1025	1205
	5	1100	1380
Catfish			
Age 1-2	Segment	Start Weight	80% end weight
	1	28	197
	2	77	180
	3	48	183
	4	34	180
	5	28	138
Age 2-3	Segment	Start Weight	80% end weight
	1	240	425
	2	205	449
	3	216	485
	4	216	485
	5	165	546
Crappie			
Age 1-2	Segment	Start Weight	80% end weight
	1	22	92
	2	14	54
	3	19	55
	4	19	64
	5	19	55
Age 2-3	Segment	Start Weight	80% end weight
	1	110	162
	2	64	134
	3	64	134
	4	75.	141
	5	64	134

in their second growing season (age-2). Channel catfish growth rates were moderate, but typical of water bodies with similar growing seasons.

Diet Analysis

The diets of the three target species were diverse and variable by species but remained uniform across reservoir segments. Walleye diets consisted primarily of fish, specifically juvenile catfish and carp, black crappie fed upon a mixture of invertebrates and fish, and channel catfish fed primarily upon aquatic vegetation and organic detritus (Table 2). Larger, adult, individuals of all target species fed upon prey fish to a greater extent than juvenile or sub-adult individuals.

Table 2. Diet proportions (blot dry wet weight) of target species. Values represent average stomach content in grams for each diet item.

Diet item	Catfish	Crappie	Walleye
carp	0.04	0.11	0.2
catfish sp.	0.03	0	0.58
chironomid	0.03	0.01	0
coleoptera	0.1	0.01	0
crappie	0.01	0.07	0.01
fathead minnow	0.01	0.16	0.04
hemiptera	0.01	0.49	0
mice	0.01	0	0
organic material	0.74	0.07	0.04
sunfish sp	0	0.01	0.02
unidentified fish	0.01	0.03	0.07

Bioenergetics Modeling

The daily growth potential of the target species varied widely according to modeled thermal conditions (Figure 4). Channel catfish growth potential peaked at 29^{o}C, and at this temperature catfish growth potential ranged from 2.75 g/day (field estimated consumption -20%) to 4.0 g/day (field estimated consumption +20%). Black crappie growth potential was greatest at 22^{o}C and ranged from 0.32 g/day (field estimated consumption -20%) to 0.45 g/day (field estimated consumption +20%) at this temperature. Peak walleye growth potential depended more strongly on the consumption rate modeled and ranged from 1.04 g/day at 17^{o}C (field estimated consumption -20%) to 3.24 g/day at 20^{o}C (field estimated consumption +20%).

Modeling results show that growth potential for the three target species varies widely by season, indicating that large changes in seasonal habitat quality occur within Cutler Reservoir (Figure 5). Black crappie and walleye growth potential peaked during spring with a second, lower peak during autumn. Both walleye and crappie experienced reductions, 103% and 99% respectively, in their average daily growth potential (g/day) from May 21 to July 30, as thermal conditions became limiting for these species. Conversely, channel catfish average daily growth potential increased by 78% during this same period, achieving the highest rates during the summer as temperatures reached the optimal range for this species across most of the reservoir. On May 21, channel catfish growth potential averaged 1.75 g/day (Figure 5a). Catfish growth potential was highest on this date in shallow shoreline habitats, where water temperatures were warmest. On July 30, catfish growth potential reached its peak with an average of 3.13 g/day, and

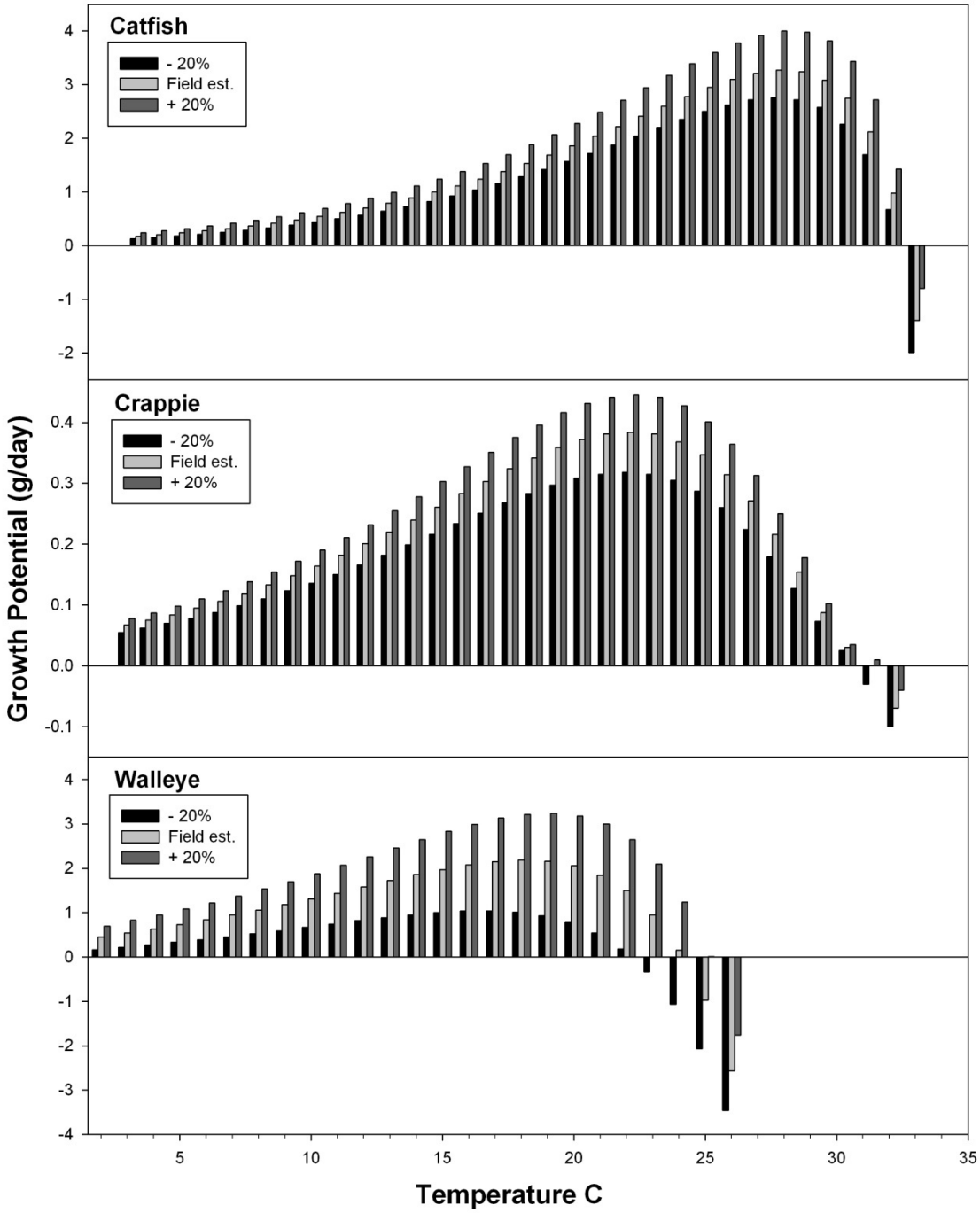

Figure 4. Growth potential curves for target species calculated using the temperature range of the study area and our bioenergetics model. Field estimated growth potential curves (in grams) for target species are shown in gray with ±20% of our estimated field consumption shown for comparison (note changes in y axis).

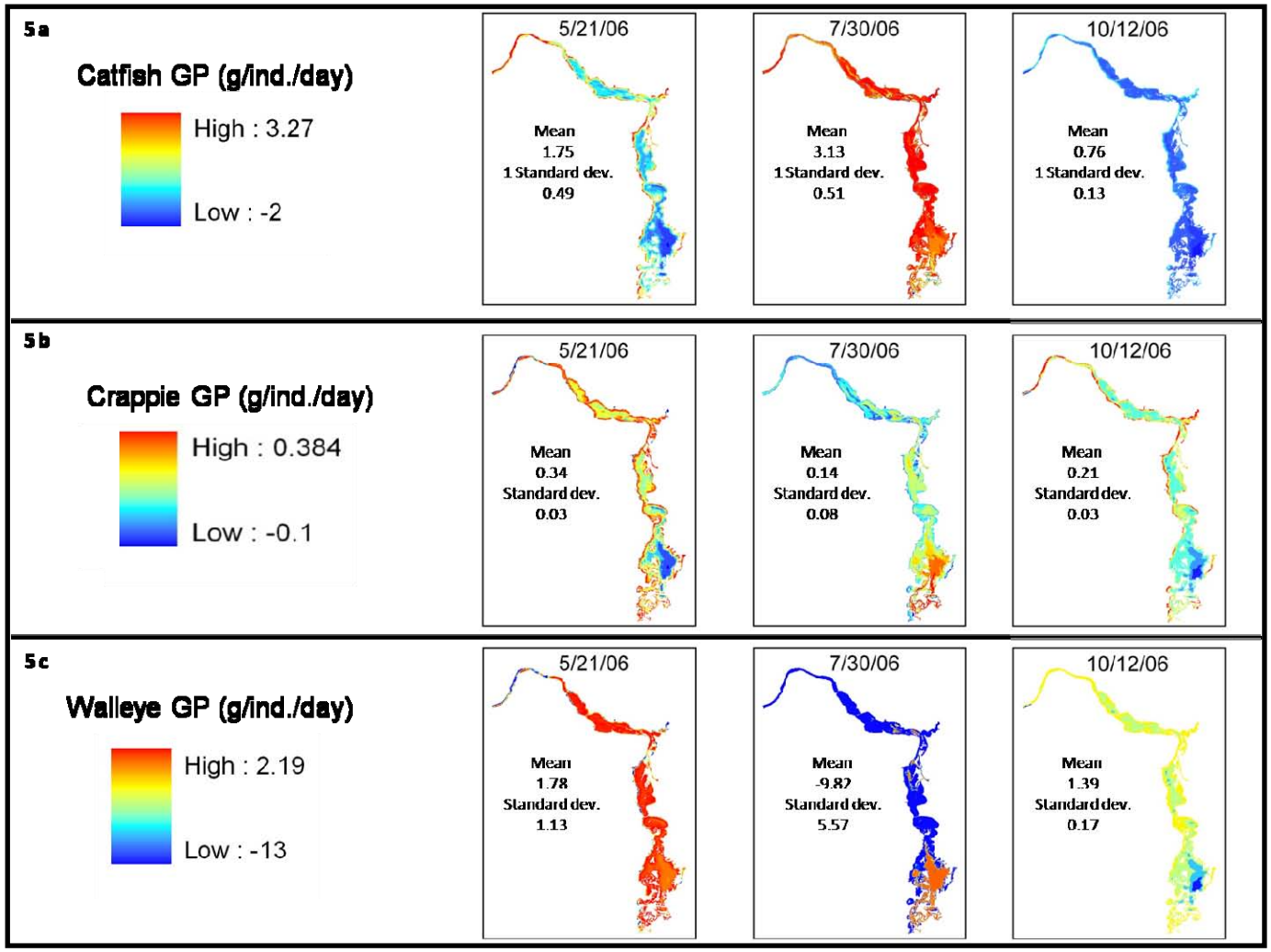

Figure 5. Seasonal growth potential of target species. Spatially defined growth potential maps (in grams) for spring, summer, and autumn of 2006. Model output represents an average individual of each target species (see text).

nearly 100% of the reservoir offered optimal growth potential for catfish during this time period. By October 12, thermal conditions had cooled below the optimal range for channel catfish throughout the water body and habitat that offered low growth potential dominated.

In contrast to the model results for channel catfish, black crappie growth potential averaged 0.34 g/day on May 21, the highest average of the modeling efforts for this species (Figure 5b). As with catfish, spring growth potential for black crappie was highest along warm shoreline habitats and lowest in the cool southern tributary inflow area. Interestingly, crappie growth potential dropped to an average of 0.14 g/day by July 30. On this date, model results indicate that habitat providing high growth potential did exist for crappie, but it was confined to the cool southern tributary inflow area that displayed the lowest growth potential during the spring. In a pattern similar to the spring, crappie growth potential was again highest along warm shoreline habitats on October 12, with an average of 0.21 g/day.

Walleye growth potential reached its highest average, 1.78 g/day, on May 21 (Figure 5c). At this time walleye growth potential was high across most of the reservoir with few areas exhibiting sub-optimal thermal conditions. By July 30, walleye growth potential had dropped to an average of -9.82 g/day. On this date most of the reservoir displayed negative growth potential for walleye except for the southern tributary segment, where walleye demonstrated positive growth potential. On October 12, walleye growth potential had climbed to an average of 1.39 g/day representing an intermediate

level between the extremes of spring and summer. Autumn walleye growth potential was greatest along warm shoreline habitats.

Cumulative Frequency Distribution (CFD) plots allow one to further investigate seasonal shifts in habitat quality for the three target species by illustrating how habitat availability changes with species-specific thermal suitability (Figure 6). In May, 60% of available habitat offered channel catfish a growth potential range of 1.24 – 2.04 g/day representing an intermediate habitat quality between the extremes of summer and autumn. Summer growth potential for catfish was high with greater than 90% of available habitat providing a growth potential above 3 g/day. Autumn catfish growth potential provided less than 20% of available habitat with a growth potential above 0-g/day. Black crappie and walleye CFD plots are similar to each other with May providing the majority of suitable habitat in the medium to high growth potential range. However, walleye display a stronger negative distribution in suitable habitat than do crappie during July, a function of this species limited physiological ability to thrive in warm water conditions.

The relationship between model-derived, site-specific seasonal growth potential and corresponding CPUE estimates is variable and inconsistent based on linear regression (Table 3). The relationship between mean growth rate potential and CPUE is generally weak for catfish and walleye. In contrast, the relationship between mean growth rate potential and CPUE for crappie is significant and positive during spring ($p = 0.007$, R2 0.93); by summer this relationship had shifted to a nearly significant negative relationship ($p=0.08$, R2 0.69).

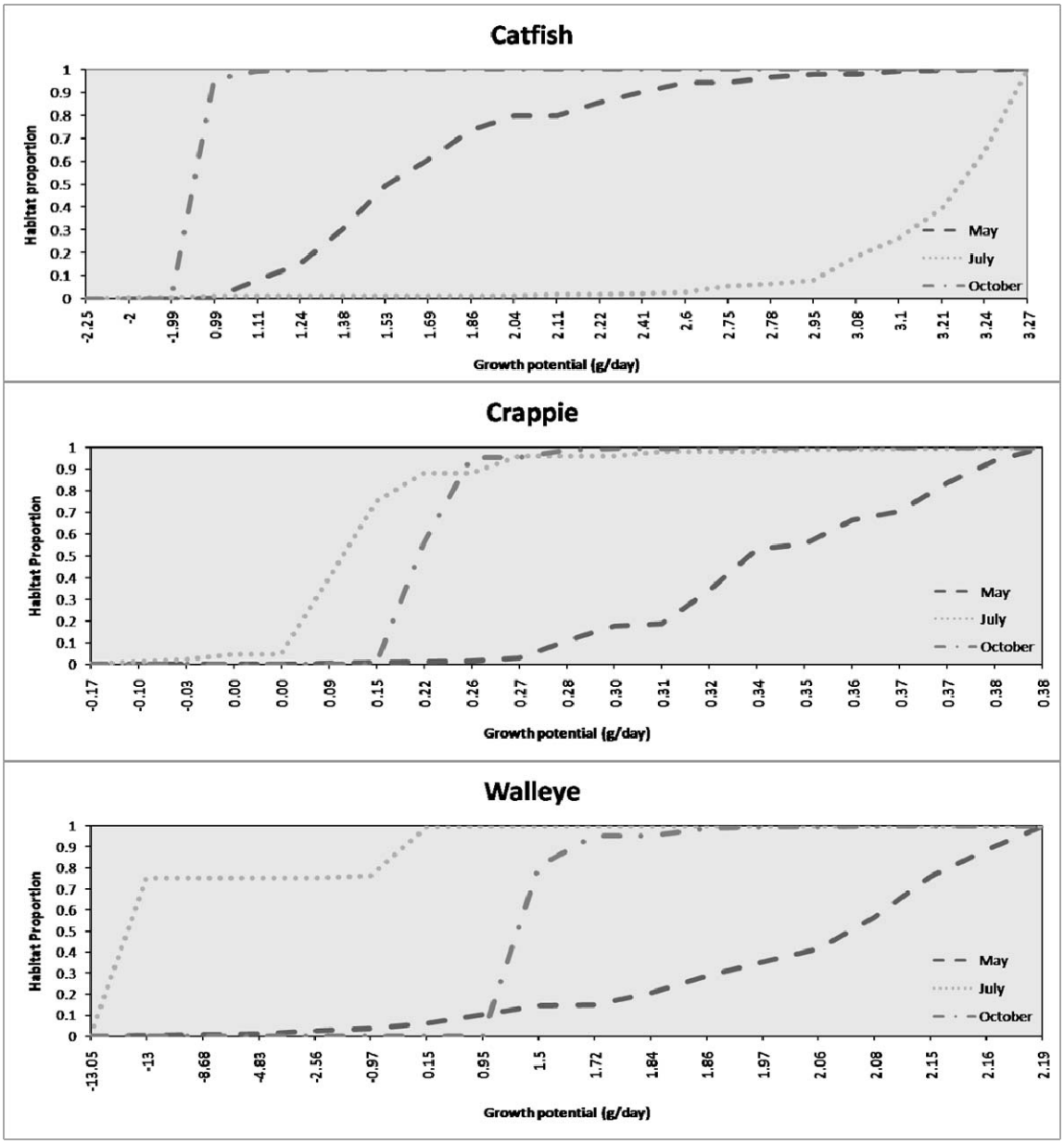

Figure 6. Cumulative Frequency Distribution (CFD) plots of habitat area and modeled growth potential for each target species.

Table 3. The relationship between growth rate potential and Catch-per-unit-effort (CPUE) based on linear regression. Average seasonal growth potential from each site was regressed against the corresponding average CPUE. CPUE units represent the number of fish captured per net hour (gill and trap net combined), α was set to 0.05 *a priori*, and n=5 (sites 1-5) for all regressions.

Season	Species	Relationship	R2	p value
Spring				
	Catfish	-	0.27	0.37
	Crappie	+	0.93	0.007
	Walleye	+	0.001	0.92
Summer				
	Catfish	+	0.03	0.77
	Crappie	-	0.69	0.08
	Walleye	-	0.41	0.24
Autumn				
	Catfish	+	0.04	0.74
	Crappie	-	0.07	0.66
	Walleye	+	0.5	0.18

DISCUSSION

In this study, our goal was to evaluate the growth potential of predominant game fishes residing in a shallow, mixed reservoir of unknown fish habitat suitability. To meet this objective, we first conducted seasonal (spring, summer, autumn) fish sampling using trap nets, gill nets, and electro fishing. We used this field information to generate growth rate and consumption estimates for use in bioenergetic modeling. Next, we defined our bioenergetic model inputs and results spatially using a GIS framework and produced seasonal synoptic views of spatially defined growth potential for the system. Based on prior anecdotal information, we were surprised to find a relatively diverse and abundant, albeit non-native, fish community within our study area. This fish community comprised 14 species, of which game-fish constituted 30% of total biomass. In addition, game-fish demonstrated high growth rates in Cutler Reservoir suggesting the system provides suitable habitat for these species. Our bioenergetic modeling revealed large seasonal changes in the amount and spatial-arrangement of high growth potential habitats and provides insight for our field observations. In particular, the model demonstrates the effect of high water temperature on habitat quality for cool-water fishes (black crappie and walleye) and contrasts these results with a warm water species (channel catfish). This study represents a novel use of bioenergetic modeling in that we were able to extend our model results to include the entire water body throughout the primary growing season while incorporating a high degree of spatial resolution (3-30 meters).

The quantification of fish growth potential incorporates both biotic and abiotic variables that impact each fish species uniquely and often fluctuate widely across space

and time (Crowder and Cooper 1982; Romare et al. 2003). As such, it is not surprising that we found the peak growth potential of our target species occurred at different times of the growing season. The model results show that black crappie and walleye growth potential peaked during spring and autumn, while channel catfish growth potential reached its highest levels during the summer period. Spatially, peak growth potential shifted from shallow shoreline habitats during spring and autumn to localized thermal refugia during summer for walleye and crappie. In contrast, catfish growth potential was high throughout the reservoir during the summer modeling period. This diversity in species-specific growth potential emphasizes the dynamic nature of fish growth potential and, ultimately, the care one must exercise when defining habitat quality (Costanza 1992).

Our results confirm that fish growth potential is tightly coupled with the thermal regime of a water body (Brandt et al. 1992; Mason et al. 1995), and to a large extent this coupling defines the habitat quality available for a specific species of fish (Power and Attrill 2007). We found that the growth potential of the target fish closely tracked the thermal characteristics of the habitat available in Cutler Reservoir, a pattern that has been noted by others in both similar and dissimilar systems (Goyke and Brandt 1993; Hughes and Grand 2000; Freidland et al. 2000). Assuming food resources were generally sufficient to support high growth rates within the study area, we expected the peak in mean growth potential of our target species to coincide with the time period when Cutler Reservoir provided the greatest amount of habitat that matched the thermal preferences of our target species. The results from our field observations and modeling support this

hypothesis. Interestingly, for both crappie and walleye, we found that a single location within the study area, the southern tributary inflow, oscillated between the lowest growth potential in the reservoir to the most energetically beneficial, providing the highest growth potential, depending on the season modeled.

Seasonal growth potential fluctuated most widely for walleye and was marked by a negative mean growth potential during the summer period. The model results for walleye suggest this species experiences a period of thermal stress with greater than 95% of the water body providing negative growth potential during the warmest portion of the growing period. Despite this finding, walleye within Cutler Reservoir maintain above-average yearly growth rates when compared to other North American recreational walleye fisheries (Radant and Sakaguchi 1979; MNDNR 2006; Quist et al. 2002). This discrepancy between model predictions of negative growth potential during warm periods and the high growth rates we measured in the field has been observed elsewhere (Luecke et al. 1999; Hook et al. 2004), and there are several possible explanations. First, spatially-explicit bioenergetics models may be inaccurate due to errors in species physiological parameters, inaccurate estimation of consumption estimates, imprecision in thermal data, or a combination of these measures (Ney 1990; 1993; Boisclair 2001). Second, the duration of the time period of negative growth potential may be too short to be of consequence, such that fish may endure a short period of negative growth while growth over the entire season remains positive (Headrick and Carline 1993). Third, fish may be capable of locating and utilizing thermal refugia that are not identified in modeling efforts (Torgerson et al. 1999). Lastly, fish may be extremely adept at utilizing

complex habitat mosaics in a manner that minimizes or eliminates periods of low growth (Luecke et al. 1999). Any one, or a combination of these factors, may explain the tendency for fish to demonstrate positive growth overall despite periods of predicted low growth potential (Tyler and Brandt 2001; Hook et al. 2004).

One enticing use of spatially-explicit bioenergetic models has been their application for predictions of fish habitat selection. However, attempts to align the output of these models with actual observations of fish distribution in the field have generated mixed results (Luecke et al. 1999; Nislow et al. 2000). The modeling approach described here relies more heavily upon thermal condition than previous spatially-explicit bioenergetics models, which may provide a better predictor of fish distribution (Wildhaber and Crowder 1990; Hook et al. 2004b; Power and Attrill 2007). Nonetheless, our CPUE estimates did not consistently agree with our spatially defined growth potential output, and the relationship was often negative. We note, however, that our metric of fish distribution has limitations for this comparison and represents only a coarse estimate of fish abundance and distribution (Post et al. 2002). Further, the lack of agreement between our metric of fish distribution and our spatially defined maps of growth potential do not necessitate a flaw in the modeling effort, as fish may select habitats based upon other factors not considered here such as spawning aggregations (Seelback 1993) or habitat partitioning (Olson et al. 1988), further disconnecting observed fish distribution from a metric of predicted growth potential. Ultimately, the static nature of current spatially defined bioenergetic models appears to limit their ability to predict the dynamic nature of fish habitat selection (Tyler and Brandt 2001; but see Nislow et al. 2000).

Future bioenergetic models that incorporate competitive interactions, deduct the costs of movement between forage patches, and document localized forage production could improve the ability of these models to accurately predict fish habitat selection (Tyler and Brandt 2001; Railsback and Harvey 2002).

The modeling approach we describe capitalizes on advanced technology in thermal remote sensing, which allows for a significant increase in the spatial resolution of a system-wide bioenergetic model. We know of only one other study that has used this approach to incorporate thermal data into a bioenergetics model. Hook et al. (2004a) used Advanced Very High Resolution (AVHR) satellite thermal remote-sensing data to generate spatially defined growth potential estimates for steelhead (*Oncorhynchus mykiss*) in Lake Michigan. Our model differs from the approach of Hook et al. (2004) in several important ways. First, we defined our model results at a much higher resolution, 9m2 cells vs. 234,000,000 m2 cells. Second, we were able to extend the model output to include the entire water column, as a function of the lack of thermal stratification in Cutler Reservoir. Mason and Brandt (1996) noted that increases in the spatial definition of model inputs improve the ability to detect extremes in habitat growth potential and reduce the tendency of model outputs to overestimate mean growth potential. Finally, we used a combination of satellite and aerial TIR imaging and validated the thermal images using in-situ temperature loggers. Recent validation of TIR imaging lends support to its use as an accurate tool for measuring the thermal properties of aquatic habitats and corroborates our findings (Handcock et al. 2006).

The improvements we achieved in spatial resolution and system-wide coverage in temperature are potentially constrained by a lack of prey distribution information. Our approach assumes a uniform distribution of prey and uses the physiological response of a fish to temperature in order to estimate consumption rate. The model results would undoubtedly change, and could improve in accuracy with the incorporation of more descriptive prey availability information and the inclusion of a foraging module (Brandt et al. 1992). Nonetheless, foraging models also require many simplifying assumptions and may not accurately represent prey availability and concomitant consumption estimates of target species (Persson and Greenberg 1990; Giske et al. 1998; Mazur and Beauchamp 2006). While the quantification of accurate consumption rates continues to present a challenge for spatially defined bioenergetics models in general, our progress in describing thermal habitat at a much finer resolution and the enhanced understanding of habitat use that has resulted should not be overlooked (Hansen et al. 1993).

The sampling conducted in this study revealed several inaccuracies in anecdotal fisheries information for Cutler Reservoir. Historical information regarding the fish community within the system is limited. However, previous spot sampling suggested that water quality in the reservoir has been impaired resulting in simplified fish community composition dominated by rough fish and with low overall fish abundance. In contrast to this anecdotal information, we captured 14 fish species and we found that a considerable percentage of biomass was comprised of game fish. Black crappie and walleye demonstrated growth rates at the upper range of reported values for these species (Carlander 1969; Quist et al. 2002; Weathers et al. 2005). Nevertheless, our findings

suggest that walleye may provide a useful target species for use in Total Maximum Daily Load (TMDL) standard determination. Walleye are a cool-water species and require relatively high levels of dissolved oxygen (>5 mg/L). Therefore walleye may provide biological relevance to the process of determining allowable nutrient loading levels by integrating habitat suitability across multiple spatial and temporal scales. Future refinements to our bioenergetics model could incorporate the response of fish to the exposure of environmental pollutants (Rajotte and Couture 2002; Sherwood et al. 2000, 2002), and nutrient perturbations (Gu et al. 1996; Vander Zanden and Rasmussen 1996), furthering the application of bioenergetics models in predicting the effects of water quality management scenarios on fish growth rates.

Spatially-explicit bioenergetics models facilitate the understanding of complex patterns in habitat quality and fish habitat use that emerge across varying spatial and temporal scales. In doing so, these models highlight the sporadic and inconsistent nature of fish growth (Roy et al. 2004). Nislow et al. (2000) noted a positive relationship between mean growth rate potential and first year survival for juvenile Atlantic salmon, while Power and Attrill (2007) observed a change in survival rates associated with thermal habitat availability for Thames estuary smelt. Both of these studies emphasize the importance of understanding spatial and temporal components of habitat quality and illustrate how key periods of fish growth have important ramifications for fish vital rates (Mason et al. 1995; Brandt et al. 2002). The approach we have described here monopolizes on readily available remote sensing data (Landsat 5) and provides a method by which mean seasonal and annual growth rate potential can be quantified using a

spatially-explicit bioenergetics model. This approach may provide an efficient means of monitoring changes in habitat quality and consequent fish production potential for economically-important fishes as well as providing guidance for conservation efforts dealing with sensitive or imperiled populations alike.

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APPENDIX

Tabel A.1. Seasonal catch biomass of common species expressed as percentage of total catch biomass.

Seasonal Catch Biomass (%)			
Species	Spring	Summer	Autumn
Carp	68.7	69.5	65.2
Catfish	18.9	17.4	19.2
Walleye	5.1	6.7	7.3
Crappie	3.5	1.2	2.2
Other	3.8	5.2	6.1

Table A.2. Seasonal CPUE, composite of all fish captured. Data represents the number of fish captured per 100 m of gill net per hour

Catch Per Unit Effort (CPUE), fish # / 100m gill net / hr Composite of all species		
Spring	Summer	Autumn
0.54	1.18	0.84